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ORIGINAL ARTICLE

Bioerosion in fossil cephalopods: a case study from the Upper Carboniferous Buckhorn Asphalt Quarry Lagerstätte, Oklahoma, USA

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Abstract

The mid-Pennsylvanian (Desmoinesian–Virgilian) deposits from the Buckhorn Asphalt Quarry Lagerstätte near Sulphur, Oklahoma, are characterized by siliciclastic–carbonate rocks. One of these deposits is the 'cephalopod coquina' that contains a large amount of orthocerid and coiled nautiloid, and ammonoid shell remains. These were used for a detailed study on bioerosion in cephalopod shells in order to help in the reconstruction of the paleoenvironment and to increase the general knowledge on bioerosion in fossil cephalopods. More than 50 shell fragments were cast and investigated. The shells cast and investigated in this study comprise a diverse set of ichnotaxa-/forms. Besides chlorophyte and cyanobacterial traces, also rhodophyte, fungal, and spongal traces are present as well as those of unknown origin. In addition, there are six ichnoforms that might have foraminiferans as producers. In orthoceratids, *Ichnoreticulina elegans* and a curly morphotype of *Scolecia* isp. are most common while the abundance in coiled cephalopods is dominated by the 'superthin form', the 'extremely thin form', and *Flagrichnus profundus*. In total, 22 ichnotaxa and -forms were recognized and 12 of these have their oldest record in the Carboniferous. The succession of ichnotaxa/-forms in the casts of orthocones suggests deposition in the deep euphotic to dysphotic zone of the Buckhorn sea while shells of coiled specimens had drifted for a while; they were therefore more prone to bioerosion by autotrophs until they sank to the seafloor.

Keywords Cephalopod shells · Desmoinesian · Foraminiferans · Nautiloidea · Ammonoidea · Bioerosion · Fossil record · Bathymetry

Introduction

The Buckhorn Asphalt Quarry deposits (Fig. 1a–e) consist of middle Pennsylvanian (Desmoinesian–Virgilian) mixed siliciclastic–carbonate, fossiliferous marine deposits of the Boggy Formation (Deese Group). These sediments represent a single cycle of transgression and regression (Seuss et al. 2009). A 'cephalopod coquina' that comprises a large amount of remains of ammonoid, and orthocerid and coiled nautiloid shell remains represents the deepest water deposits within this cycle (Seuss et al. 2009; Niko et al. 2018). Other deposits in the quarry contain a diverse marine fauna including, e.g., gastropods (most diverse and abundant), bivalves, brachiopods, foraminifers, bryozoans, and a rather diverse fish fauna (e.g., Seuss et al. 2009; Ernst et al. 2016; Ivanov et al. 2017) including so far unknown taxa. The largest benthic organisms in the outcrop are chaetetid sponges (Seuss et al. 2014) and large naticopsid gastropods with shell diameters of up to 10 cm.

The cephalopod fauna from the quarry was comprehensively studied by Smith (1938) and Boardman et al. (1994). Recently, Niko et al. (2018) have updated the taxonomy of straight nautiloids. Other studies that contain various information on the Buckhorn cephalopods are presented by Bechtel (1962), Unklesbay (1962), Ristedt (1971), Crick (1982), Chatelain (1984), Gregoire (1988), Blind (1991), Kulicki et al. (2002), Seuss et al. (2012a, b), and others.

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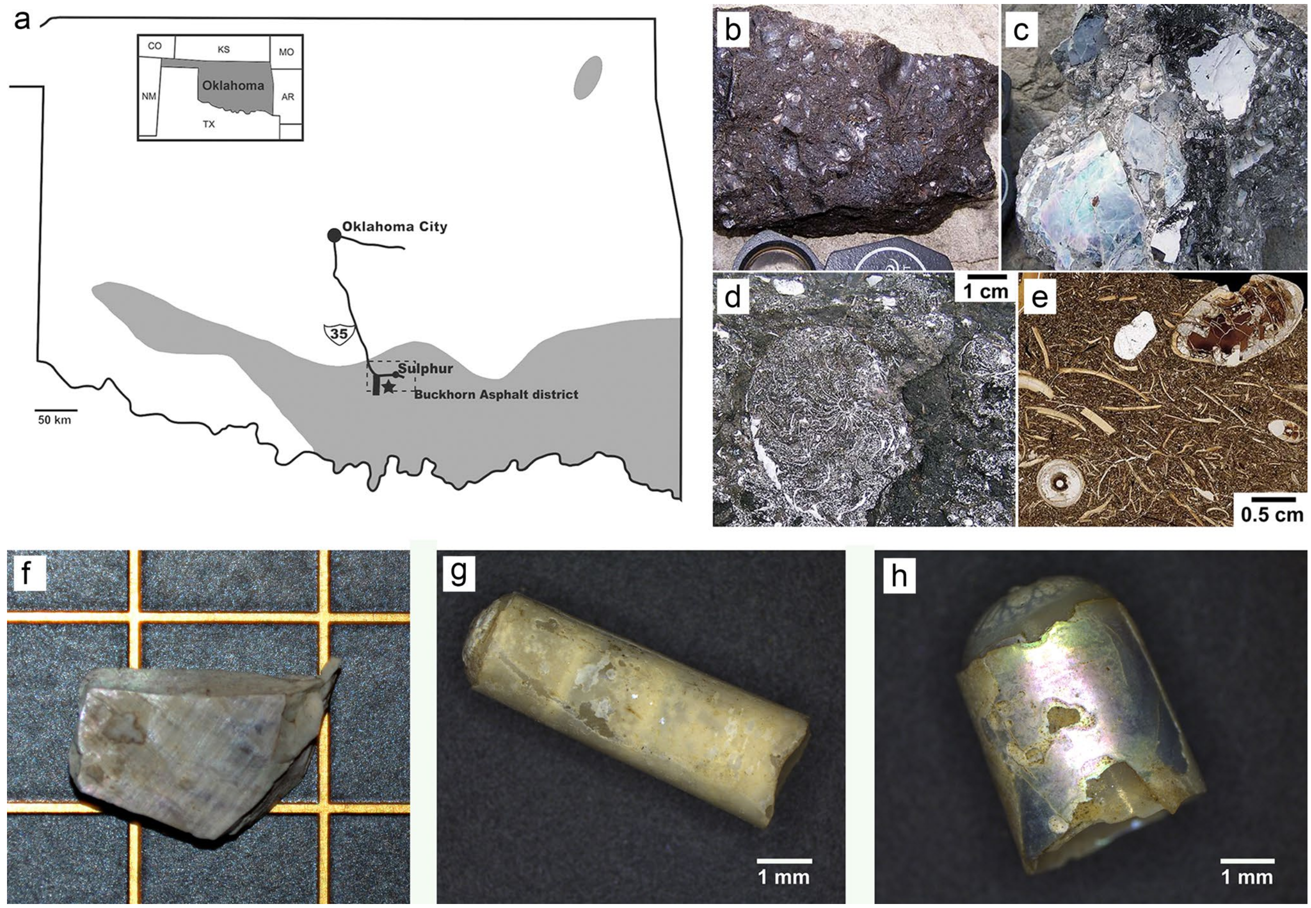

Fig. 1 Buckhorn Asphalt Quarry—site, deposits, and cephalopods. **a** Outcrops of asphaltic beds (greyish); position of the Buckhorn Asphalt Quarry marked with a star (from Ernst et al. 2016, Fig. 1A). **b–e** The 'cephalopod shell coquina' (photos from Seuss et al. 2009). **b** Freshly broken rock fragment of the 'cephalopod shell coquina', dark stained due to its high content of asphalt. **c** The 'cephalopod shell coquina' with numerous well-preserved (nacre) fragments of cephalopods. **d** Coiled nautiloid in the 'cephalopod shell coquina'. **e** Thin-section of the 'cephalopod shell coquina' with cross sections of an orthoconic (lower left) and coiled (upper right) cephalopod. **f–h** Examples of shell remains of cephalopods used to prepare synthetic resin casts (for **f**: squares are 1 cm^2)

The quality of the preservation of the fossils is, in part, outstanding; delicate shell structures like larval shells (Seuss et al. 2009, 2012c) and shell ornamentation, color patterns, or original shell material are conserved; the quarry is one of the very few Paleozoic occurrences of mollusk shells preserved in their original aragonitic composition (Seuss et al. 2009). This exceptional preservation is caused by impregnation with hydrocarbons at or only shortly after deposition of the sediments (e.g., Ham 1969; Wisshak et al. 2008; Seuss et al. 2009). The hydrocarbons have filled pore space, and tunnels and cavities produced by bioeroding organisms. Over time, the hydrocarbons and their organic components were transformed to asphalt losing its volatiles, hardening, but still preventing strong diagenetic effects.

Due to this excellent preservation, the Buckhorn Asphalt deposits have also yielded pivotal information on bioerosion in mollusks and the evolutionary history of bioeroding organisms (Wisshak et al. 2008). These authors reported 19 ichnospecies, which is the most diverse Paleozoic microboring assemblage ever reported. Their study was largely based on epoxy resin casts from gastropod and bivalve shells, while only five remains of cephalopods (ammonoids, nautiloids) were included. The latter contained six ichnospecies/-forms out of 19.

Here, we provide the first detailed study on bioerosion in fossil cephalopods (ammonoids, orthoconic, and coiled nautiloids) from the Buckhorn Asphalt Quarry in order to appraise if the depth of deposition can be evaluated by analysis of ichnotaxa in shells of ancient cephalopods. All other extended studies of bioerosion in cephalopods (i.e., in living *Nautilus*) were performed by Seuss et al. (2015a, b, 2016). They reported a diverse set of ichnotaxa including new ichnospecies and reconstructed the transport of the shells by the comparison of trace fossil assemblages.

Materials and methods

More than 50 shell fragments (Fig. 1f–h) of straight and coiled cephalopods from the Buckhorn Asphalt Quarry Lagerstätte were investigated regarding their bioerosion inventory. Thirty-two of these derive from orthoconic nautiloids and 28 are from coiled specimens (nautiloids and ammonoids). Due to heavy fragmentation of the shells, it was not possible to differentiate between nautiloid and ammonoid fragments. The conchs of straight nautiloids were all less than 1 cm in diameter (Fig. 1g, h). Fragments of coiled nautiloids and goniatites, respectively, were less than 1.5 cm across and only a few hundred microns in thickness (Fig. 1f). Results (only cephalopod data) from the earlier study on bioerosion in shell remains from the Buckhorn Asphalt Quarry (Wisshak et al. 2008) are included in the list of ichnotaxa and the discussion.

Preparation of samples (i.e., ‘cast embedding method’) followed Golubic et al. (1983) and Wisshak (2012). In short, the procedure is as follows: The samples were cleaned in an ultrasonic bath. After drying, they were placed on a base of synthetic resin in silicon bins. The bins were then inserted in a specially designed vacuum chamber (Struers Epovac) to prepare casts with synthetic resin (Giessharz wasserklar hardener and resin, mixing ratio 100:37). After the resin had hardened the shell carbonate was dissolved with diluted hydrochloric acid. The casts were rinsed with distilled water, dried, and glued onto SEM stubs. After being sputter-coated with gold, they were documented with a scanning electron microscope (Tescan Vega//xmu).

The interpretation of fossil traces is based on an actualistic approach. This means that knowledge from studies on recent material is transferred to the past by comparing the shape of modern traces with ancient ones—this is because the producer of a trace strongly resembles the shape of the boring it produces (e.g., Radtke 1991; Wilmotte and Golubic 1991; Glaub et al. 2007). Since environmental demands such as trophodynamics, salinity, temperature, and relative water depth, i.e., the dependence on sunlight (see Wisshak 2012 for a review) are known for recent producers, this information is transferred to reconstruct conditions of the past.

In ichnotaxonomy, recent endolithic organisms either follow the International Code of Zoological Nomenclature (ICZN; International Commission on Zoological Nomenclature 1999) or the International Code of Botanical Nomenclature (ICBN 2000), while the traces they produce are covered by the ICZN, exclusively (Wisshak et al. 2005). For fossil taxa, it is, in our opinion, reasonable to list both, the producer (known/inferred) and the ichnotaxon (i.e., the produced trace) (compare Table 1). In addition, we have listed the substrate they occur in as well as their relative abundance.

The synthetic resin casts are hosted in the Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany) under collection numbers SNSB-BSPG 2011 X 235 to SNSB-BSPG 2011 X 294.

Results: ichnotaxa and -forms in the casts

In the following, the occurring ichnotaxa and -forms are listed according to their abundance in the casts.

Ichnoreticulina elegans (Radtke and Golubic, 2005)

Figure 2a, i.

Description *Ichnoreticulina elegans* penetrates the substrate as approximately 3-µm-thin galleries, which build a substrate-parallel network. The cross section is oval (i.e., only slightly flattened). Galleries extend for several tens to more than 100 µm in length on the casts surface.

Remarks Producer of the trace is *Ostreobium quekettii* Bornet and Flahault, 1889, a siphonal alga (e.g., Kornmann and Sahling 1980). This alga is very common in the deep euphotic zone but, as only representative of chlorophytes, it is found down in dysphotic zone and therefore, it is used as a key bathymetric species (Glaub 1994).

Stratigraphic range: Ordovician to the Recent (Glaub and Vogel 2004; Wisshak et al. 2008).

Curly type of *Scolecia* isp.,

Figure 2b–d.

Description Two morphologies of *Scolecia* are present in the casts. This new morphotype forms galleries of several tens to hundreds of microns in length. The diameter of single galleries is 1–2 µm. Bifurcations were not observed. Most characteristic for this trace is the curly appearance; the galleries make curves of up to 180°. The traces show now imprints of the shell nacre indicating that they spread out parallel to the substrate surface and do not penetrate vertically. Another indicator is, in our opinion, that the traces meander on the cast’s surface but are not curled up in one place. If the traces would have been vertical in orientation, some should have collapsed during dissolution of the shell carbonate and we would expect that at least some would build an accumulation of curled up traces comparable to a bowl of spaghetti.

Remarks Because the general characteristics of this trace are very similar to *Scolecia filosa*, we assign this trace as new morphotype but refrain from creating a new ichnotaxon until

Table 1 Ichnotaxon inventory in order of abundance as recorded in epoxy resin casts. Known/inferred Recent tracemaker(s)

Ichnotaxon	Known/inferred trace maker(s)	Organism	BAQ[a]	ON	CC
Ichnoreticulina elegans (Radtke and Golubic, 2005)	*Ostreobium quekettii* Bornet and Flahault, 1889	cl	o	++	+
Scolecia isp. (curly morphotype)	Cyanobacteria?	cy?	o	++	–
'Extremely thin form' sensu Seuss et al., 2015a	? Conchocelis-stage of *Porphyra* sp. or *Bangia* sp.	rh	o	+	++
'Superthin form' sensu Wisshak et al., 2011)	Unknown organotroph	h	o	+	++
Flagrichnus profundus Wisshak and Porter, 2006	*Schizochytrium sp.*	fu	o	+	++
Planobola macrogata Schmidt, 1992	Unicellular cyanobacteria	cy	x	–	+
Fascichnus dactylus (Radtke, 1991)	e.g., *Hyella caespitosa* Bornet and Flahault, 1889; *Solentia foveolarum* Ercegovic, 1927 emend. 1932; *S. achromatica* Ercegovic, 1932	cy	x	o	–
"Cavernula profunda" Radtke et al., 2011	Probably cyanobacteria	cy?	o	o	+
'Floating tire'-form	Foraminifer?	fo?	o	o	–
Saccomorpha clava Radtke, 1991	*Dodgella priscus* Zebrowski, 1937	fu	o	–	–
Eurygonum nodosum Schmidt, 1992	*Mastigocoleus testarum* Lagerheim, 1886	cy	x	o	–
Planobola macrogata (flattened morphotype)	Unicellular cyanobacteria?	?	o	o	–
Scolecia filosa Radtke, 1991	*Plectonema terebrans* Bornet and Flauhault, 1889; *P. endolithicum* Ercegovic, 1932	cy	o	o	–
Fascichnus frutex (Radtke, 1991)	*Hyella gigas* Lukas and Golubic, 1983	cy	o	–	–
? Polyactina fastigata Radtke, 1991	Unknown (probably heterotroph)	fu?	o	–	o
'Macaroon'-form	Foraminifer?	fo?	o	o	–
'Acetabulum'-form	Foraminifer?	fo?	o	–	o
'Spongia'-form	Foraminifer?	fo?	o	–	o
'Snowball'-form	Foraminifer?	fo?	o	–	o
'Loculi'-form	Foraminifer?	fo?	o	–	o
Scolecia serrata Radkte, 1991, spheroidal form	Unknown organotroph (bacteria?)	ba?	o	–	o
Entobia isp.	*Cliona* or other Hadromerida	po	o	–	o
Cavernula coccidia Glaub, 1994	Probably cyanobacteria	cy?	x	o	o
Rhopalia catenata Radtke, 1991	*Phaeophila dendroides* (Crouan) Batters, 1902	cl	x	o	o
'Palaeoconchocelis starmachii'	*Porphyra nereocystis* Anderson in Blankinship and Keeler, 1892	rh	x	o	o

[a] Study of Wisshak et al. (2008). Organism that made the trace (known or inferred): *cy* cyanobacteria, *cl* chlorophyte, *rh* rhodophyte, *po* porifera, *fu* fungus, *fo* foraminifera, *h* heterotroph, *?* unknown. *CC* coiled nautiloid/ammonoid), *ON* orthoconic nautiloid. Relative abundance to each other (++: very common, +: common, o: not present, -: rare, –: very rare)

there are more findings of this ichnoform. The resemblance to *S. filosa* suggests some cyanobacterium as producer.

Stratigraphic range Upper Carboniferous.

'Extremely thin form' sensu Seuss et al., 2015a

Figure 2e.

Description This trace is characterized by extremely thin (less than 1 mm), straight tunnels without any branching or creating a meshwork (note that this is different to the 'superthin form') or any other structures resembling sacks, spheres, etc. The length is several tens up to 100 µm and more.

Remarks The producer of this ichnoform is unknown.

Stratigraphic range Upper Carboniferous, Recent (Seuss et al. 2015a).

'Superthin form' sensu Wisshak et al. (2011)

Figure 2f.

Description Traces of this kind are characterized by thin galleries of uniform diameter (less than 1 µm) and a length of several tens of microns. In the casts they are largely unbranched but occasionally, bifurcations occur, as do swellings. In this study, the nacreous structure of the cephalopod shell is visible as imprints indicating that the producer was penetrating vertically into the substrate.

Remarks According to Wisshak et al. (2011), the trace is produced by some so far undetermined organotroph.

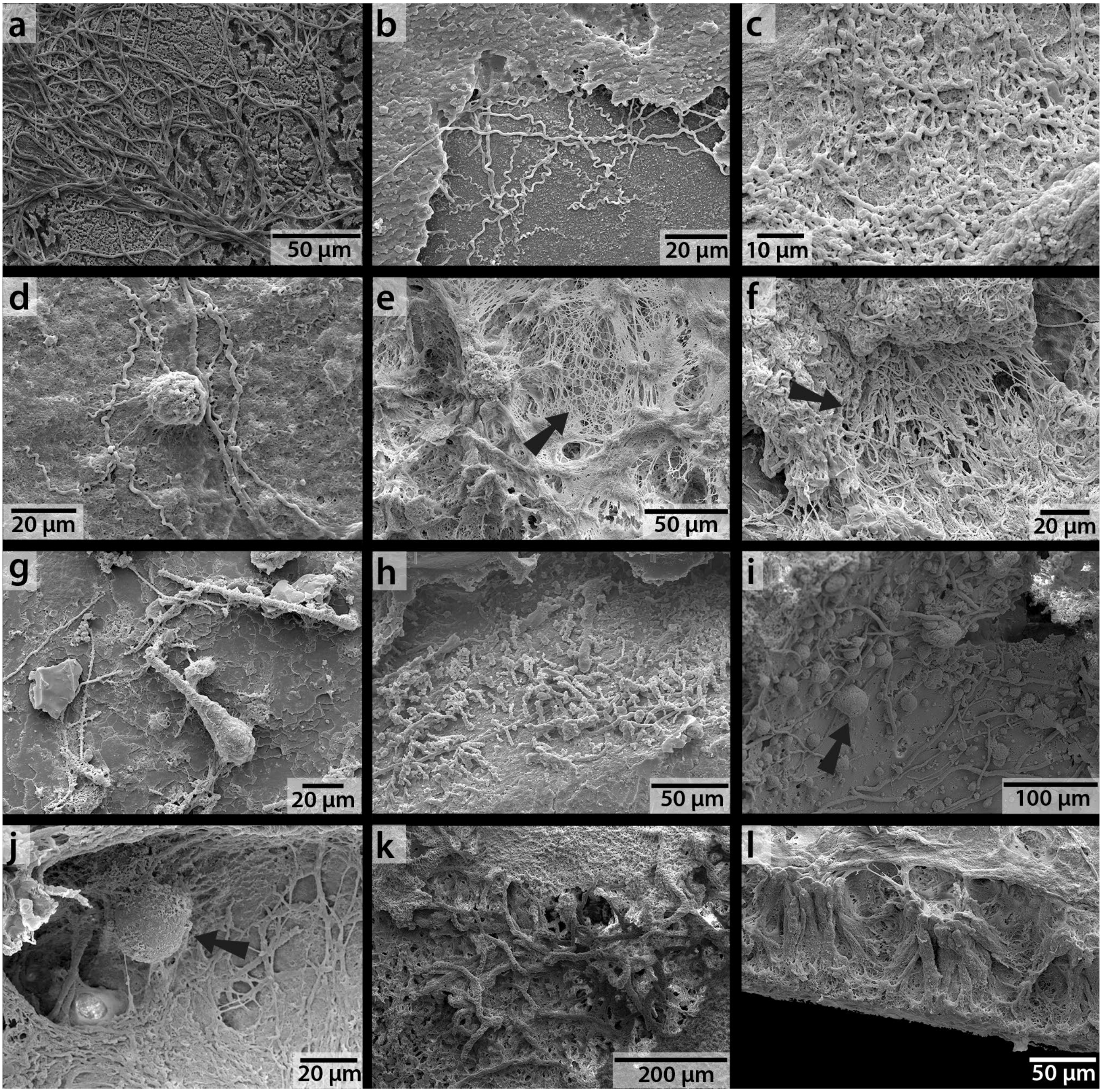

Fig. 2 SEM photos of casts of fossil traces in cephalopods from the Buckhorn Asphalt Quarry. **a** Accumulation of the chlorophyte trace *Ichnoreticulina elegans*. **b–d** Morphotype of *Scolecia* isp. with curly appearance, likely produced by cyanobacteria. **d** Curly *Scolecia* and the spherical fungal trace *Saccomorpha clava*. **e** An accumulation of the 'extremely thin form'. **f** The heterotroph trace 'superthin form' forming a dense meshwork (arrow) of tunnels. **g–h** *Flagrichnus profundus*, produced by a fungus (**g** colony of *F. profundus*; **g** isolated trace, enlarged); whips lost by preparation. **i–j** *Planobola macrogata*. **i** Traces of a colony of *P. macrogata* (arrow) produced by some unicellular cyanobacterium in association with *Fascichnus dactylus* (cyanobacterial; thicker tunnels) and *I. elegans* (thinner tunnels). **j** Single specimen of *P. macrogata*. **k–l** Views onto *Fascichnus dactylus*. **k** *Fascichnus dactylus* in plan view. **l** *F. dactylus* in side view

Stratigraphic range Upper Carboniferous, Recent (Wisshak et al. 2011).

Flagrichnus profundus **Wisshak and Porter,** 2006

Figure 2g, h.

Description Flagrichnus profundus is characterized by its whip-shaped form. The initial part of the trace has a diameter of up to 22 µm, while the whip has a diameter of 3–4 µm only; the trace penetrates deeply into the substrate in a perpendicular manner. The galleries reach a length of several tens of microns; however, preparation caused loss of length of many whips in our samples. The trace occurs in clusters of several tens of specimens and in different ontogenetic stages.

Remarks Producer of the trace in recent settings is the fungus *Schizochytrium* sp.

Stratigraphic range Upper Carboniferous, Recent (Wisshak and Porter 2006).

Planobola macrogata **Schmidt, 1992**

Figure 2i, j.

Description Planobola macrogata is present as characteristic semi-spherical to spherical trace with diameters of up to 50 µm. The surface or trace does not show any further features. Clusters of *P. macrogata* are common in the casts.

Remarks There are a few possible producers of this trace. Most plausible are unicellular cyanobacteria (e.g., *Chroococcus* and *Cyanosaccus*). Alternatively, the sporophyte phase of chlorophytes or fungal zoospores are considered to produce *P. macrogata* (Glaub 1994).

Stratigraphic range Silurian, Upper Carboniferous to the Recent (Glaub and Vogel 2004; Wisshak et al. 2008).

Fascichnus dactylus **(Radtke, 1991)**

Figures 2i, k, l.

Description The galleries of *Fascichnus dactylus* are thin (4–8 µm in diameter) and they penetrate the substrate oblique to perpendicular. Bifurcations are very rare. From the initial spot of penetration, the galleries begin to radiate.

Remarks In the Recent various endolithic cyanobacteria produce this trace; most common is *Hyella caespitosa* Bornet and Flahault, 1889 (e.g., Radtke 1991; Gektidis 1997); *Solentia foveolarum* Ercegovic 1927 emend. 1932 or *Solentia achromatica* Ercegovic, 1932 also produce *F. dactylus.*

Stratigraphic range Ordovician, Upper Carboniferous to the Recent (Glaub and Vogel 2004; Wisshak et al. 2008).

"*Cavernula profunda*" Radtke et al., 2011

Figure 3a, b.

Description The borings in the Buckhorn cephalopods are comprised by a 50–60 µm long, initially 5 µm and towards the tip 14–18 µm in diameter, club-shaped part and a whip/tail of more than 100 µm in length. In the casts, imprints of the shell nacre are well visible pointing to the fact that penetration of the substrate was vertical.

Remarks The producer is unknown, but Radtke et al. (2011) suggest a pleurocapsalean cyanobacterium as trace maker.

Stratigraphic range Upper Carboniferous, Recent (Radtke et al. 2011).

'Floating tire'-forms

Figure 3c–f.

Description There are two morphotypes in the casts that are assigned to the 'floating tire'-form. Traces of the larger form (Fig. 3c, d) are circular and 150–160 µm across. The penetration depth is approximately 20–25 µm. The shape resembles this of a floating tire; the depression in the center has a diameter of 35–40 µm. In broken specimens the internal organization is visible showing a rather regular meshwork that shows radial "galleries" that are connected by shorter ones.

The small form (Fig. 3e, f) resembles the larger one in that way that it also has the shape of a floating tire. However, this trace is much smaller with only 60 µm in diameter. The penetration depth is approximately 20 µm. The depression in the middle of the small form is less pronounced, if present, and not as roundish. The specimens show a meshwork-like structure, as is observed in the large form. It seems that the trace is not only surrounded by but also sits above other traces and that it is not embedded like the large form is. However, this is not clearly visible because other traces cover the base and the impression might be the result of intense bioerosion by other specimens. Some of the specimens show an additional feature; i.e., a thin gallery surrounds the tire-shaped part half way from base to top (Fig. 3f). It is possible that the large and the small form represent different ontogenetic stages of one and the same trace maker.

Remarks Because such traces are unknown so far, the producer cannot be determined. For both morphotypes a foraminiferan origin is suggested (also see "Discussion").

Stratigraphic range Upper Carboniferous.

Saccomorpha clava **Radtke, 1991**

Figures 2d, 3 g.

Description Saccomorpha clava has a club- to sack-shaped morphology (10–20 µm in length) and interconnecting substrate-parallel galleries. In the casts, the traces often occur as clusters of several dozens of specimens.

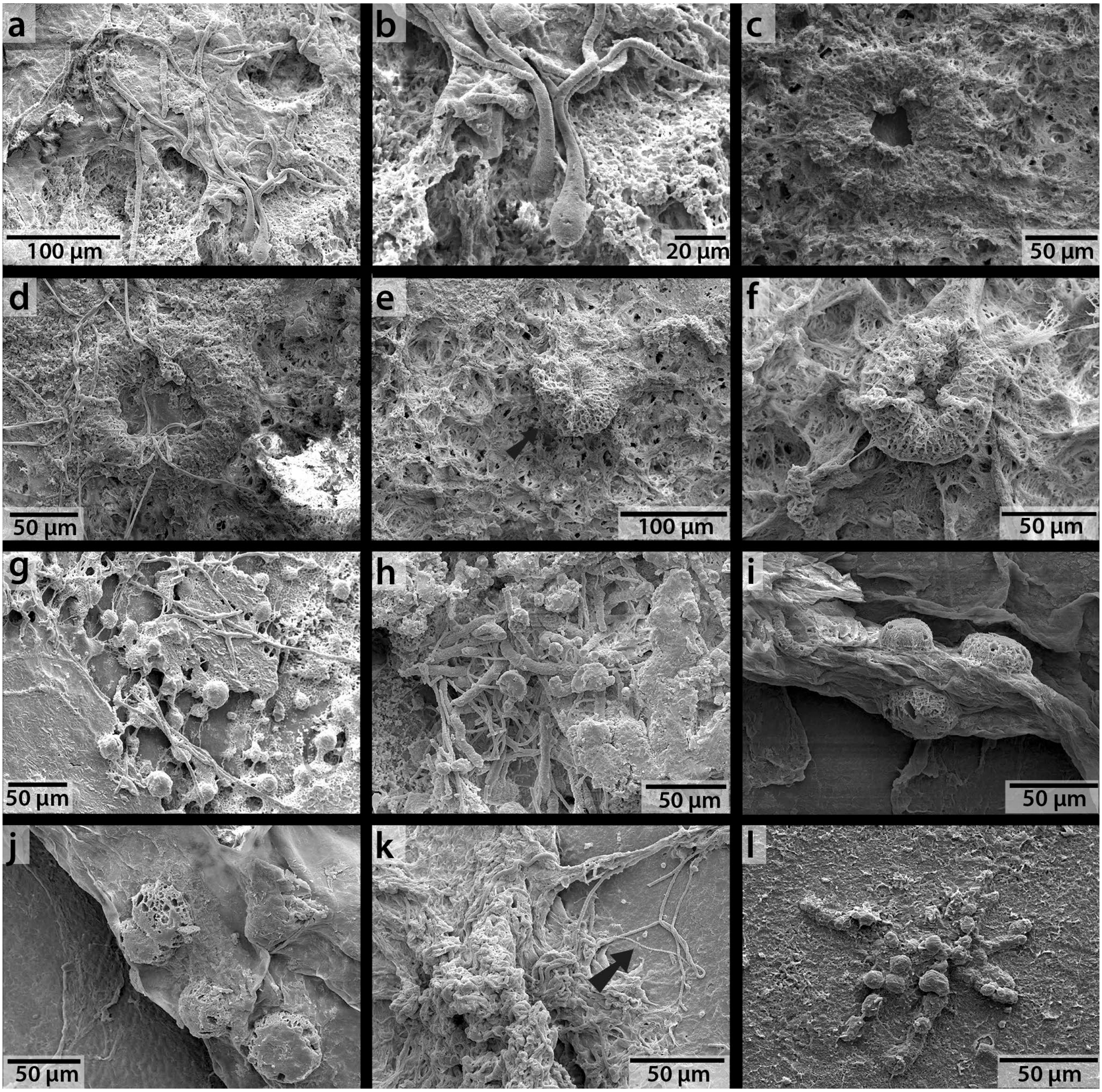

Fig. 3 SEM photos of casts of fossil traces in cephalopods from the Buckhorn Asphalt Quarry. **a–b** "*Cavernula profunda*" produced by a cyanobacterium (**b** is the close-up of **a**; imprints of nacre are visible). **c–f** Traces of the 'floating tire'-form. **c–d** Large morphotype; internal structure of the trace well visible, a mesh-like structure, due to the lack of the rounded part as preserved in **d**. **e** Small 'floating tire'-morphotype with nicely preserved mesh-like internal structure. **f** Trace of the small 'floating tire'-form with nicely preserved mesh-like internal structure and rim (*arrow* in **e**). **g** The spherical fungal trace *Saccomorpha clava* appearing in a cluster. **h** The poorly preserved cyanobacterial trace *Eurygonum nodosum.* **i–j** Flattened morphotype of *Planobola* isp. **k** Rare occurrence of *Scolecia filosa* (*arrow*). **l** The cyanobacterial trace *Fascichnus frutex*

Remarks The producer in recent settings is the marine fungus *Dodgella priscus* Zebrowski, 1936, which is most common in aphotic settings (e.g., Zebrowski 1936; Zeff and Perkins 1979; Budd and Perkins 1980; Radtke 1991). *Saccomorpha clava* is used as key ichnospecies for the aphotic zone in combination with *Orthogonum lineare* (Glaub 1994).

Stratigraphic range Ordovician, Carboniferous to Cenozoic (Glaub and Vogel 2004; Wisshak et al. 2008).

***Eurygonum nodosum* Schmidt, 1992**

Figure 3h.

Description Eurygonum nodosum consists of three-dimensional networks of galleries. The diameter of the galleries is of 4–6 µm only. Nodular appendices or swellings and dichotomous branching was rarely observed; the shape of the terminations of the galleries varied from round to blunt. *E. nodosum* networks can reach up to several 100 µm into the substrate.

Remarks Producer of the trace in modern environments is *Mastigocoleus testarum* Lagerheim, 1886 (e.g., Radtke 1991; Gektidis 1997).

Stratigraphic range Upper Carboniferous to Jurassic, Quaternary to the Recent (Glaub and Vogel 2004; Wisshak et al. 2008).

Planobola **isp. (flattened morphotype)**

Figure 3i, j.

Description Planobola isp. has a diameter of up to 45 µm at a penetration depth of 15–20 µm. The surface of the spheres is homogenous. Broken spheres show a hollow, which indicates that some substrate was initially filling them prior to treatment with acid to dissolve the cephalopods shell carbonate. This morphotype was found in clusters of a few specimens but occurred isolated as well. Compared to *P. macrogata* it is flattened.

Remarks Such traces have not been reported before, therefore the producer is unknown. Because of the resemblance with *P. macrogata* (Fig. 2i, j), we refrain from assigning it to a new ichnotaxon until more traces of this kind are found.

Stratigraphic range Upper Carboniferous.

Scolecia filosa **Radtke, 1991**

Figure 3k.

Description The galleries of *Scolecia filosa* have diameters of 1-2 µm only. Because of a length of several tens of microns, they are usually found collapsed on the cast surface. Bifurcations occur occasionally.

Remarks Plectonema terebrans (e.g., Bornet and Flahault 1889; Perkins and Tsentas 1976; Radtke 1991) and *P. endolithicum* Ercegovic, 1932 (see Glaub 1994) are known to produce this trace in modern settings. The ichnotaxon is used for paleobathymetric interpretations (i.e., as indicator for the dysphotic zone).

Stratigraphic range Ordovician to Silurian, Upper Carboniferous to the Recent (Glaub and Vogel 2004; Wisshak et al. 2008).

Fascichnus frutex **(Radtke, 1991)**

Figure 3l.

Description F. frutex consists of a set of tunnels that radiate from the spot of entrance. The tunnels widen and bifurcate at their distal, blunt ends. The diameter is up to 25 µm at the tips of the tunnels. Diameter of the entire colonies in the Buckhorn casts is 600 µm at maximum.

Remarks Producer of the trace is the cyanobacterium *Hyella gigas* (Lukas and Golubic 1983).

Stratigraphic range Proterozoic, Ordovician to Silurian, Upper Carboniferous to the Recent (Glaub and Vogel 2004; Wisshak et al. 2008).

cf. *Polyactina fastigata* Radtke, 1991

Figure 4a.

Description P. fastigata is characterized by a substrate-parallel, dendritic meshwork of borings (8–15 µm in diameter). This meshwork is created by dichotomously ramifying galleries of varying angle. The galleries emerge from a single central cavity or an elongated gallery and taper towards their terminations.

Remarks The producer of this trace is unknown, likely it has a heterotroph origin.

Stratigraphic range Upper Carboniferous, Paleogene-Recent (Radtke 1991; Wisshak et al. 2008).

'Macaroon'-form

Figure 4b.

Description Traces of this type are characterized by a circular outline and a diameter of 110–160 µm. The penetration depth is 10–20 µm. The surface has a characteristic structure that consists of roundish (~ 10 µm in diameter) elevated spots that appear to be arranged in an irregular circle with one single spot in their middle.

Remarks The producer of this trace is unknown and such trace has not been reported so far. We suggest a foraminiferan origin with the trace being the etching (see "Discussion").

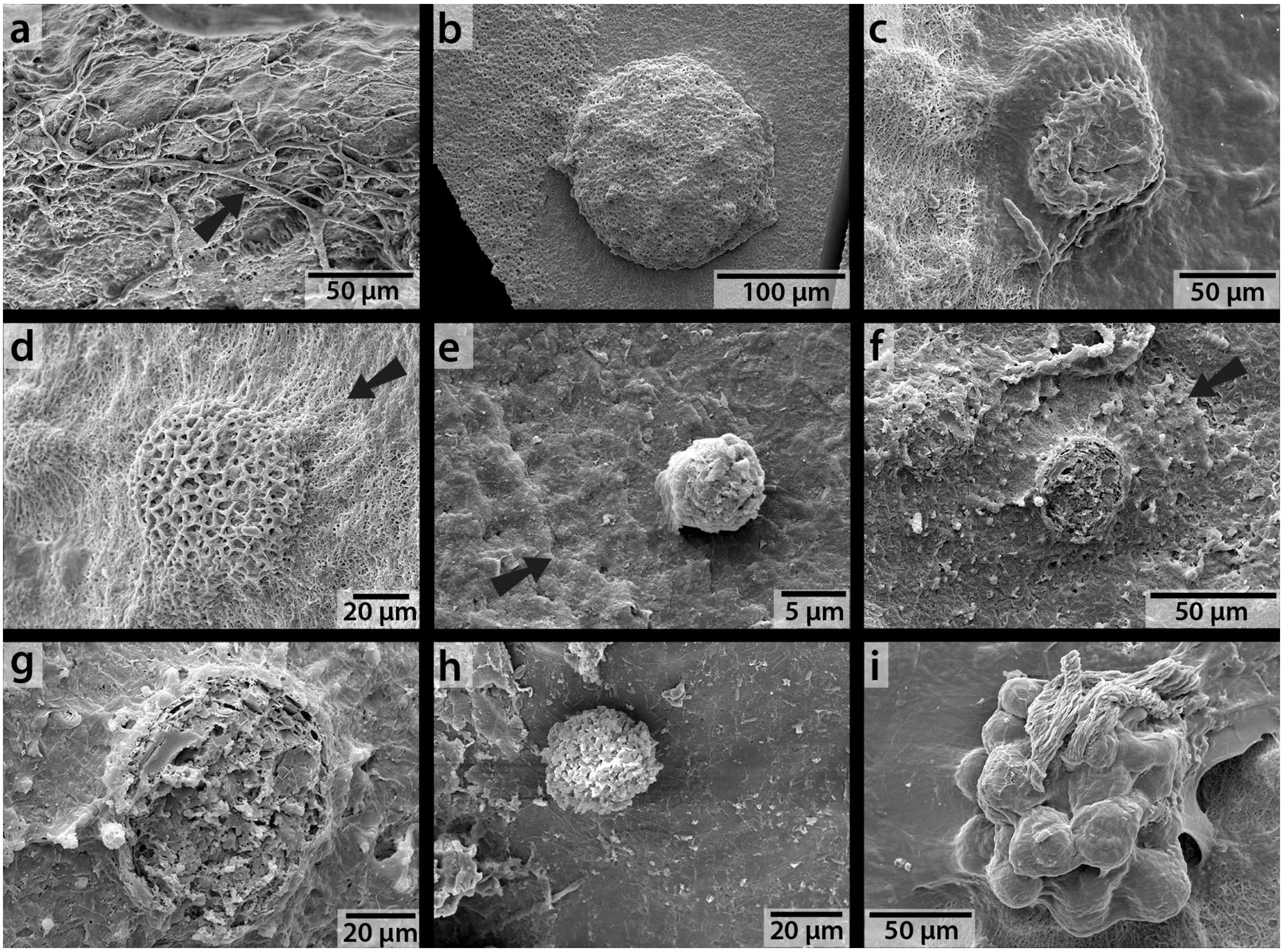

Fig. 4 SEM photos of casts of fossil traces in cephalopods from the Buckhorn Asphalt Quarry. **a** cf. *Polyactina fastigata* indicated with an *arrow*. **b** Flat, circular trace with short, roundish elevations representing the 'macaroon'-form. **c** The 'acetabulum'-form with broader base and a ring-like structure. **d** The 'spongia'-form with an inner mesh-like structure and an outer depressed rim. **e** The 'snowball'-form, a spherical inner part and a radial, chambered rim. **f–g** The 'loculi'-form with an inner chambered area and an outer depression. **g** Close-up of the inner area of the 'loculi'-form with chamber-like structure (**f**). **h** A spherical appearance of *Scolecia serrata*, producer is some bacterium. **i** Characteristic form of *Entobia* isp. produced by a sponge

Stratigraphic range Upper Carboniferous.

'Acetabulum'-form

Figure 4c.

Description The trace described as 'acetabulum'-form has a base of 125 µm across and a second level resembling a tire of 75 µm in diameter. The penetration depth of the levels is 15 µm and 10–12 µm, respectively. The second level has a depression in its middle. The outline of the entire trace is rather circular.

Remarks The producer of the trace is unknown, but we suggest a foraminiferid as borer (see "Discussion").

Stratigraphic range Upper Carboniferous.

'Spongia'-form

Figure 4d.

Description A ring-shaped rim and an inner circular part compose the 'spongia'-form. The 30-µm-wide rim is a depression that shows a week radial ray-like pattern. The inner part has a diameter of approximately 60–65 µm at a depth of 20 µm and shows a distinct meshwork-like structure.

Remarks The producer is unknown. As before, we suggest that the trace was produced by a foraminiferid (see "Discussion").

Stratigraphic range Upper Carboniferous.

‘Snowball’-form

Figure 4e.

Description This small trace consists of a spherical inner structure that is surrounded by an only weak pronounced rim. The sphere has a diameter of only 6–8 µm and the rim appears to be of spiral organization. The surface of the sphere is slightly serrate.

Remarks The producer of this kind of trace is unknown. We suggest a foraminiferid (see “Discussion”).

Stratigraphic range Upper Carboniferous.

‘Loculi’-form

Figures 4f, g.

Description The ‘loculi’-form contains an inner part and an outer rim. The inner part has a diameter of 40 µm and the entire trace is approximately 100 µm across. The rim is depressed; the inner part shows a pronounced mesh-like structure that resembles chambers of a spherical object.

Remarks The trace maker is unknown; as for other new traces in this study we suggest, based on the appearance, a foraminiferid (see “Discussion”).

Stratigraphic range Upper Carboniferous.

Scolecia serrata Radkte, 1991, spheroidal form

Figure 4h.

Description Scolecia serrata was found as a single, spherical structure of 40 µm in diameter. The surface of the sphere shows the characteristic serrate micro-sculpture of individual *S. serrata* galleries. *S. serrata* seems to have overgrown a no more identifiable spherical trace, e.g., *P. macrogata*.

Remarks The producer of *S. serrata* is still unknown. It is suggested that it is produced by bacteria (e.g., Zeff and Perkins 1979; Budd and Perkins 1980; Young and Nelson 1988). In any case, the producer must be organotrophic because traces of *S. serrata* are found in aphotic depths (e.g., Radtke 1991; Wisshak 2006). *Scolecia serrata* is a well-known trace; however, spherical occurrences are only reported by Seuss et al. (2016) so far.

Stratigraphic range Upper Carboniferous, Cenozoic (Radtke 1991; Wisshak et al. 2008).

Entobia isp.

Figure 4i.

Description The single specimen of *Entobia* in the casts appears in its characteristically raspberry shape that is the result of penetrating the substrate by removal of chips. Diameter of the boring is 100 × 150 µm with numerous knob-like protrusions of 35–45 µm in diameter.

Remarks Producers of such traces are *Cliona* and other kinds of hadromerid sponges.

Stratigraphic range Cambrian to Recent (Wisshak 2012).

Other microborings

Traces that were found in cephalopod shells in the initial study on bioerosion in shells from the Buckhorn Asphalt Quarry (Wisshak et al. 2008) but not in this study are as follows:

- *Cavernula coccidia* Glaub, 1994 (producer: probably cyanobacteria; stratigraphic range: Upper Carboniferous, Triassic to the Recent, Glaub 1994 and Wisshak et al. 2008),
- *Rhopalia catenata* Radtke, 1991 (producer: *Phaeophila dendroides* (Crouan) Batters, 1902; stratigraphic range: Upper Carboniferous to the Recent, Glaub and Vogel 2004 and Wisshak et al. 2008), and
- ‘*Palaeoconchocelis starmachii*’ Campbell, Kasmierczak and Golubic, 1979; stratigraphic range: Silurian, Upper Carboniferous-Jurassic and Paleogene-Recent, Campbell et al. 1979 and Glaub and Vogel 2004).

Discussion

The new study contains at least 22 ichnotaxa-/forms, which create a diverse ichnoinventory (Table 1). Most common are *Ichnoreticulina elegans* and the curly morphotype of *Scolecia* in casts of orthoconic nautiloids, while most common ichnotaxa/-forms in coiled cephalopods are the ‘extremely thin form’, the ‘superthin form’, and *Flagrichnus profundus*. The assemblage from this study contains eight new ichnoforms: one morphotype of *Scolecia* and *Planobola* each, and six presumable foraminifer traces. There are 12 oldest appearances discovered in the Buckhorn Asphalt Quarry cephalopods, which are the eight new ichnoforms along with “*Cavernula profunda*”, *Fascichnus profundus*, and the 'extremely thin' and 'superthin' forms (see above and Table 2).

The trace fossil assemblage of the orthoconic specimens contains 15 ichnotaxa/-forms (Table 1). Of these, five traces of autotroph organisms are present only (three cyanobacteria, and one chlorophyte and rhodophyte each). All other traces derive from heterotrophs. The coiled cephalopods show different content (Table 1): 15 ichnotaxa/-forms occur, but nine of these derive from autotroph producers, five from heterotrophs, and one is unknown. For both types of cephalopods, we considered the foraminiferans as producers counting them as heterotrophs. Adding the six known ichnotaxa-/forms discovered in cephalopods by Wisshak et al. (2008), the trace set yields a total of 25 ichnotaxa/-forms recorded in cephalopod shells from the Buckhorn Asphalt Quarry. Among the traces in cephalopods that were listed by Wisshak et al. (2008), five derive from autotrophs and one either from an auto- or a heterotroph organism.

There are structures that could not be clearly be identified as traces of any bioeroding species or specimen. These structures, which occur in a few but not in all of the casts, have a fibrous structure that might cover a distinct area. Examples are seen in e.g., Figs. 3c, 4c, d. Such and a similar structure (e.g., Fig. 2k, 4b) are present in both orthoconic and coiled cephalopods. Golubic et al. (2016) illustrated the surface of a coastal limestone that is bioeroded by cyanobacteria. The surface resembles the structures in Figs. 2k and 4b to some extent. The authors report that grazing on the limestone's surface by invertebrates has accordingly caused truncations; therefore the surface structure was modified. A comparison of a limestone surface and a cast's surface might be meaningless at first glance, the one being the substrate, and the other being the mold; however, one has to keep in mind that not only penetrating organisms will affect what we see in the Recent and fossil record but also grazers (Schneider 1976; Schneider and Torunski 1983) and thus, a comparison is complimentary.

Diversity

Diversity in the casts of the Buckhorn Asphalt Quarry cephalopods is very high. Adding the ichnotaxa/-forms that were recovered in shells of gastropods and bivalves, in total 32 ichnotaxa and -forms are known from the Buckhorn Asphalt Quarry now (Table 2) and 25 of these occur in cephalopod shells (Table 1). This is the most diverse assemblage of ichnotaxa known from the entire Paleozoic and the present study adds considerably to the diversity reported by Wisshak et al. (2008).

Diversity in the cephalopod shells differs from those in the non-cephalopods; eight traces that were recorded in gastropod and bivalve shells in 2008 do not occur in shells of Buckhorn cephalopods. On the other side, 13 of the reported ichnotaxa and new forms from this new study do not occur in the casts from the initial study. This implies that either the depositional environment for gastropods/bivalves and cephalopods was different or that there was specialization among the borers, i.e., some organisms had preferred the shell of cephalopods. The facts are: (1) sedimentological data show that the cephalopods derive from a different setting within the transgressive–regressive cycle of sediments exposed in the quarry (compare Seuss et al. 2009, Fig. 6) (also see "Discussion" later); (2) the sample that contains the highest number of gastropods and bivalves contains only very few remains of cephalopods and the other way around; (3) all studied shells belong to mollusks. Considering these facts, one might conclude that there is a mix of sedimentological influence along with some specialization among the microboring organisms—this refrains hypothetical, however. There are eight ichnoforms recorded in this study that have not been reported so far, i.e., not from the fossil record and not from modern settings. Therefore, it may be speculated that these taxa might have been specialized on (Paleozoic) cephalopods and are not found in the Recent because orthoconic and most of the coiled nautiloids (except the extant *Allonautilus* and *Nautilus*) as well as goniatites (ammonoids) became extinct. Consequently, microborers adapted to this kind of substratum also became extinct. The comparison with the studies of Seuss et al. (2015a, b, 2016) revealed that only 11 ichnospecies occur in both the Buckhorn cephalopod and the *Nautilus* casts and from the latter, only *Semidendrina pulchra* was not found in the fossil cephalopod shells (Table 2). However, 19 ichnotaxa are recorded in extant *Nautilus* but not in the Buckhorn Asphalt Quarry and at least nine (four of them of foraminiferan origin) are exclusive to *Nautilus* (compare Seuss et al. 2015a, b, 2016 and tables therein; Table 2). A preliminary investigation of cephalopod bioerosion reported in the literature shows that most specimens studied are belemnites. The vast majority of ichnotaxa/-forms are reported from the Mesozoic on and only very few were also reported for Paleozoic cephalopods. This and the above-mentioned difference, as of now, supports the idea that ichnotaxa are lost with the extinction of the Paleozoic cephalopods.

Traces of foraminiferan origin

Naked foraminifers are not preserved in the fossil record as their organic body underlies fast decay. Therefore, to be sure about the origin of the traces reported herein, an analogue in the Recent is required. The chance of being preserved is much higher for encrusting foraminifers. However, transport and movement on the sediment before being embedded might also destroy the tests of such. In this study, the outermost shell layer of the cephalopods was lost, and with it potential encrusting foraminifers.

Table 2 Occurrences of ichnotaxa in the Buckhorn Asphalt Quarry sorted alphabetically including the study by Wisshak et al. (2008) and this one; the three *Nautilus* studies (Seuss et al. 2015a, b, 2016) are also listed as comparison

Ichnotaxon/-form	Wisshak et al. 2008	This study	In *Nautilus*
'Acetabulum'-form		**New**	
Aurimorpha varia	New		
Cavernula coccidia	**Oldest**		
Cavernula pediculata	Oldest		
"Cavernula profunda"		**Oldest**	
'Conchocelis'-stage			2016
'Cluster-form'			2015a
'Disk-form'			2015a
Entobia isp.		**x**	
Entobia isp. (not *Entobia* in this study)			2015a
Entobia nana			2015a
Eurygonum nodosum	**Oldest**	**x**	2015a
Eurygonum pennaforme			2015a
'Extremely thin form'		**Oldest**	2015a
Fascichnus cf. *acinosus*			2015a
Fascichnus dactylus	**First**	**x**	2015a
Fascichnus frutex	First	**x**	2015a (cf.)
Fascichnus grandis			2015a
Fascichnus rogus	x		
'Flagellum-form'			2015a
'Floating tire'-form		**New**	
Flagrichnus profundus		**Oldest**	2015a, 2016
Ichnoreticulina elegans	x	**x**	2015a, 2016
'Loculi'-form		**New**	
'Macaroon'-form		**New**	
'Morphotype 1'			2015a, b
'Morphotype 2'			2015b
'Morphotype 3'			2015a, b
'Morphotype 4'			2015a, b
'*Orthogonum* form 1'			2015a
Orthogonum fusiferum	x		
Orthogonum lineare			2015a
'Palaeoconchocelis starmachii'	**First**		
Planobola isp.			2015a
Planobola isp., flattened type		**New**	
Planobola macrogata	**First**	**x**	2015a
cf. *Polyactina araneola*			2015a
Polyactina fastigata	Oldest	**x**	
Rhopalia catenata	**Oldest**		2015a
Rhopalia clavigera			2015a
Rhopalia spinosa	Oldest		
Saccomorpha clava	x	**x**	2015a
'*Saccomorpha* form'			2015a
Saccomorpha terminalis	Oldest		
Scolecia isp., curly type		**New**	
Scolecia filosa	x	**x**	2015a, 2016
Scolecia serrata	Oldest	**x**	2015a, 2016
Semidendrina pulchra	x		2015a
'Snowball'-form		**New**	
'Spongia'-form		**New**	
'Superthin form'		**Oldest**	2015a, 2016

x indicates presence of the trace in the assemblage of ichnotaxa/-forms from the Buckhorn Asphalt Quarry; *bold* indicates occurrences in fossil cephalopods

Six traces were presumably produced by foraminiferans. The assignment to foraminiferid producers is based on the following observations: (1) the size of most of the traces in question rules out most other producers, e.g., bacteria, fungi, chlorophytes; (2) for some of these ichnoforms, the internal structure (e.g., systems of chambers, mesh-like structure we call 'spongial') of the traces as well as their shape (e.g., circular rims, radially increasing diameter) point to, in our opinion, foraminiferid producers; (3) the size of the traces would fit to sponges as producers as well, but these are rejected because the characteristic raspberry-like surface is not present in those Buckhorn borings with assumed foraminiferid origin; (4) personal communication with Max Wisshak and reliance to his expertise as well as records in earlier studies on *Nautilus* (Seuss et al. 2015a, b, 2016).

We understand that we do need an analogue in the Recent to be convinced that these traces were produced by foraminiferans, if we follow the actualistic approach. Therefore, we preliminary assign them to foraminiferans but use open nomenclature that mirrors the characteristic of the trace leaving their origin open to further discussion. In the following, the individual traces are addressed. The 'floating tire'-form (Fig. 3c–f) is large and therefore numerous producers can be excluded. The shape, even the size would fit, excludes sponges as they have their characteristic shape and surface. The trace has no resemblance with any other known trace. The 'macaroon'-form (Fig. 4b) is similar to the echinoid trace *Circuloites* that is reported by Buatois et al. (2017, fig. 63c). However, the Buckhorn trace differs distinctly in size and in the presence of numerous small knobs on its surface. Therefore, we exclude an echinoid origin but suggest a foraminiferid origin instead. This is supported by similarity with the illustration of *Oichnus simplex*, which is supposed to have foraminiferan origin (Wisshak 2008, fig. 2c). The 'acetabulum'-form (Fig. 4c) has some similarity with the trace *Globodendrina monile* (Plewes et al. 1993, pl. 1, figs. 1, 2). Plewes et al. (1993) illustrate the agglutinated chimney of a specimen; considering that the 'acetabulum'-form in the present material is a foraminifer as well, the ring-shaped part of our trace might be some comparable structure. The 'spongia'-form (Fig. 4d) distinctly resembles *Gypsina* (e.g., Wisshak and Rüggeberg 2006; Wisshak 2006; Wisshak et al. 2011). Therefore, we also suggest foraminiferan origin for the Buckhorn boring. We are not aware of any other *Gypsina*-like trace not being produced by a foraminifer. The 'snowball'-form (Fig. 4e) is small in contrast to our previous statement on the size of foraminiferid traces above. However, in the middle of the trace, a radial structure with septa-like appearance is observed, which surrounds a sphere and that increases radially in size. This could be interpreted as the sphere being representative of the soft body of the specimen etching into the substrate while the radial part is produced by the shell of an (encrusting) foraminifer with only a part of the soft body sitting in the substrate while most of it remained in the test. The 'loculi'-form (Fig. 4f, g) resembles 'Morphotype 2' reported by Seuss et al. (2015b, fig. 3D), which is proven to be produced by an encrusting foraminifer. The middle spherical part shows a spiral organization of rectangular chambers (Fig. 4g) resembling an organization that is well known from foraminifers. Because of the distinct likeness with a recent trace and the internal organization, we also suggest the 'loculi'-form to be produced by a foraminifer.

Nautiloids and ammonoids probably had a periostracum that was strong enough to protect the shell from most bioeroders. Anyhow, Seuss et al. (2015b) have shown evidence that *Nautilus* is bioeroded by foraminiferans and it is reasonable that some Paleozoic foraminiferid taxa had the ability to penetrate the periostracum in order to access the shell. So far, Seuss et al. (2015a, b, 2016) have provided the only extensive study on bioerosion in cephalopods i.e., in *Nautilus* shells. Therefore, there is a great chance that further research will result in the discovery of more boring foraminifers in the Paleozoic and in cephalopods. The present finding of as many as six traces possibly produced by foraminiferans is unusual. The higher diversity of presumable foraminiferid borings in Paleozoic nautiloid and ammonoid shells could reflect the much higher diversity of ectocochleate cephalopods in the Paleozoic especially when compared with Recent ones (only the genera *Nautilus* and *Allonautilus* are still present today).

There is a considerable number of publications on boring foraminifers in the literature. Traces were, for example, reported by Baumfalk and Nijholt (1984), Vénec-Peyré (1985, 1988), Cherchi and Schroeder (1991), Kołodziej (1997), Beuck et al. (2008), Bromley et al. (2007), Wisshak et al. (2005, 2011, 2014), Wisshak (2008), Vogel and Brett (2009), or Walker et al. (2017). However, none of the traces resembles those from the Buckhorn Asphalt Quarry.

Traces of foraminifers that have bored into cephalopod shells were also reported. Examples are in Quenstedt (1849), Mägdefrau (1937), Pugaczewska (1965), Nadjin (1969), Kutscher (1972), Marcinowski (1972), Radwański (1972), Hofmann (1996), Reich and Frenzel (2002), Glaub (2004), Hosgör and Kosták (2012), Taylor et al. (2013), or Wisshak et al. (2017). These traces, except for *Semidendrina pulchra* (in Seuss et al. 2015a) occur in the rostrum, an internal structure, of belemnites; this means that these traces were most likely produced post mortem. So far Seuss et al. (2015b; Morphotypes 1–4) were the only ones to report traces that derive from foraminifers in externally shelled cephalopods, i.e., in extant *Nautilus* with the traces exclusively produced during lifetime. These foraminifers had the ability to penetrate the periostracum, an organic layer that is prone to abrasion (Seuss et al. 2015b): the older it is, the thinner this layer will be, as is well visible on shells of *Nautilus*. One may conclude, that this is also valid for fossil nautiloids and ammonoids. Borings reported and illustrated by the above-mentioned authors (except for 'Morphotype 2' in Seuss et al. 2015b) have no similarity with those reported herein.

Mode of life of bioeroders and timing of bioerosion

Seuss et al. (2015b) could show that foraminiferans are able to penetrate the periostracum during lifetime of the extant *Nautilus*. Successful penetration might strongly depend on the thickness of the periostracum. The purpose of boring is also crucial (e.g., habitat or nutrients/food). Parasitic foraminifers are well known (see summary by Walker et al. 2017) and therefore, should be considered in this study even though the oldest known foraminiferan parasites are known from the Cretaceous so far (Walker et al. 2017). Because of the lack of a recent analogue to our presumable foraminiferan traces, only vague conclusions can be drawn on the purpose. The traces are extremely rare and small (compared to their hosts); we therefore suggest that these bioeroders were not parasitic in that way that they might also have killed their host but might have well been cadgers and specimens seeking for habitat. The latter is especially reasonable for foraminiferans without test seeking for a safe place to live.

Autotrophic organisms might have penetrated the periostracum of the cephalopod specimens seeking for substrate to attach with their soft body parts. Because they required light to survive, some part of the organism will have still stuck out of the substrate. This is not the same for heterotrophs; these could have penetrated the periostracum, if having the ability to do so, to reach the internal conch seeking for substrate and food without the need to leave parts that would still gain light. In comparison with the studies on extant *Nautilus*, we as of now conclude, that only foraminiferans could penetrate the periostracum during lifetime of the specimens. Tests, however, were not found and therefore, it is unknown whether producers lacked tests or whether tests of encrusting specimens are not preserved. According to the shape and imprints, encrusting taxa could have produced the 'snowball' and the 'loculi'-forms.

Transport and deposition of the cephalopod shells

Since ectocochleate cephalopods contain a system of chambers and siphuncle to maintain buoyancy in the water column, post-mortem transport of their shells needs to be considered and therefore the results and the interpretation of these might be biased. The conchs of orthocone nautiloids, in contrast to coiled cephalopods, have cameral deposits that fill up extended parts of the phragmocone to maintain buoyancy. Thus, such conchs might not drift as far as coiled cephalopods, while the shells of coiled specimens might have floated for days to months and over large distances until they sank to the seafloor (compare *Nautilus* in Seuss et al. 2015a, b, 2016).

In respect to the ichnobathymetrical scheme (Glaub 1994; Vogel et al. 1995; Wisshak 2012), sedimentological indicators, and what we know from the extant *Nautilus*, we might speculate about the paleobathymetric setting summing up the information we have gathered from this study.

The trace fossil assemblage found in orthocone cephalopods does not comprise any key ichnotaxa that are indicative for euphotic zones 'shallow I–III'. *Ichnoreticulina elegans* is very abundant and is accompanied by rhodophytes and a few occurrences of *Saccomorpha clava*, the latter being assigned as an index fossil for the dysphotic zone with only 0.01–1% surface illumination. The orientation of the traces is largely horizontal, the diversity of ichnotaxa/-forms is rather high, and the diversity of heterotrophs is higher than those of the autotrophs. We therefore suggest deposition of the conchs in the deep euphotic to dysphotic zone. The trace fossil assemblage in the casts prepared from coiled specimens is entirely different compared with the orthocones. Most abundant are the 'extremely thin form', the 'superthin form', and *F. profundus*; these are either rhodophyte traces or produced by heterotrophs. Among the autotrophs only *I. elegans*, *P. macrogata* and "*C. profunda*" occur in moderate quantities. Traces are oriented vertically and horizontally, there are more autotrophs than heterotrophs, and an abundance of key ichnotaxa is not observed. These results make it difficult to assign the shells to a certain relative paleo-water depth. We may conclude, because of the presence of *F. dactylus*, *S. clava* and the higher content of autotrophs, that the shells of coiled species drifted for a while, this close to the water surface, being settled by autotrophs before they sunk to the seafloor.

Conclusions

The cephalopod shells from the BAQ are intensively bioeroded. More than 20 ichnotaxa/-forms are reported in this new study. Together with those from the study of Wisshak et al. (2008), including gastropods and bivalves, a total of 32 (25 of these occur in cephalopod shells) traces are known from the Buckhorn Asphalt Quarry now. This underlines the importance of the Buckhorn Asphalt Quarry as Lagerstätte and as holding the most diverse Paleozoic microboring assemblage known so far. As outlined previously (Wisshak et al. 2008; Seuss et al. 2009), this high diversity reflects a preservational window due to early sealing of mollusk shell by hydrocarbons. Eight ichnoforms in this study have not been reported so far and are presumably new. In addition to these new traces, for four ichnoforms the record was extended back into the Carboniferous. Six of the new ichnotaxa might have foraminiferan origin, which would be an extremely high number and has not been reported before so far (even from modern assemblages).

The trace fossil assemblages in the studied cephalopod shells suggest that orthocones with endocameral deposits sank rapidly and were deposited in a deep euphotic to dysphotic setting, while shells of coiled cephalopods drifted for a while before they sank to the seafloor.

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